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HYBRIDS AMONG SPECIES OF SPIROGYRA[1]

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Conjugation between filaments of different species of *Spirogyra* have been reported by several students of the algæ. Bessey (1884) reported and figured zygospores formed by the crossing of *S. majuscula* and *S. protecta.* He noted that the spores formed by the cross in either direction corresponded to the spore type of the female filament. This has been confirmed by all subsequent observers and we shall see later that this is a necessary result of the process of fertilization as it occurs in *Spirogyra.* This cross is of particular interest because the vegetative cells of *majuscula* have plain end walls, while those of *protecta* have replicate end walls. Consequently there is nothing in the physiology of these two species, representative of the two divisions of the genus, that interferes with conjugation. Wolle (1888) figures a cross between *S. maxima* and *S. ? nitida* under the name of *S. maxima* var. *inæqualis.* West and West (1898) figured a cross between two of the smaller species of *Spirogyra* but did not give their names. Andrews (1911) figured and described a cross between *S. crassa,* one of our largest species, with several chromatophores in each cell, and *S. communis,* one of the smallest of our species, with a single chromatophore. Here again the spore formed resembles that normal to the female filament. Evidently differences in size, in number of chromatophores, shape of zygospore, and character of the end walls of the vegetative cells are not impediments to crossing. In the collections from central Illinois which I have studied I have found hybrid zygospores formed between three pairs of species: *S. communis* × *S. varians* from one locality, *S. varians* × *S. porticalis* from two localities, and *S. maxima* × *S. submaxima* from one locality.

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[1] Papers from the Department of Botany, The Ohio State University, No. 104.

The phenomenon of hybridization in this genus is evidently quite rare, as shown both by the small number of references to it in the literature and by the few cases that have come under my observation. From the collections made in Illinois, Massachusetts, Michigan, Ohio and New York, I have 854 records of conjugating *Spirogyras* and only five records of conjugation between different species from four localities, all in central Illinois.

In this paper I wish to record, not only the finding of conjugation between species, but what seem to be the progeny of such crosses. It has been found impossible to cultivate these forms in the laboratory so that there is no experimental proof of their origin. Nevertheless, they have been found associated with filaments that were crossing and with filaments of the two parent species that were conjugating normally. There were few other species present in these collections, and there are no species in central Illinois that could possibly be confused with them. Under the circumstances it seems impossible to account for the strange mixture of forms in these five collections except on the basis of a hybrid origin.

Spirogyra varians × *S. communis*

In collections taken from Campus Creek, two miles southwest of Charleston, Ill., during the latter part of May, 1913, specimens of typical *S. varians* and *S. communis* occur together with filaments that resembled one or the other of these species but whose dimensions exclude them from these species. In going over these collections in 1915 filaments of *varians* were found conjugating with *communis,* and hybrid zygospores were found in both kinds of filaments. This suggested that the unnamable forms were the progeny of hybrid zygospores.

S. varians has vegetative cells .30–40 μ × 30–120 μ, a single chromatophore making one to five turns in the cell.

The sporiferous cell is usually inflated on the conjugating side and the spores are frequently placed obliquely. In conjugating filaments cells that fail to mate usually become greatly distended. The spores are ellipsoid, 32–40 μ × 50–100 μ (Fig. 1). This species is highly variable, but I have examined many collections containing it and have seen none that resemble the hybrids.

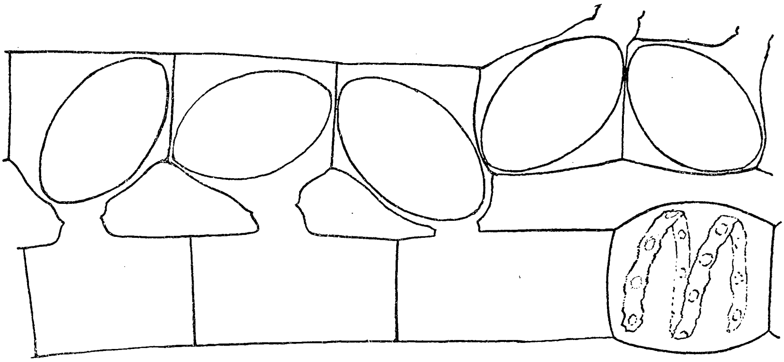

FIG. 1. Typical *S. varians* showing spore form, sporiferous cells inflated on the conjugating side, and an inflated sterile cell. Camera lucida drawing, same scale as the succeeding figures.

S. communis has vegetative cells 18–26 μ × 35–90 μ, a single chromatophore making two to four turns in the cell. The sporiferous cell is cylindrical and the spores are placed longitudinally in the cells. Cells in conjugating filaments that fail to mate usually remain cylindrical. The spores are ellipsoid, 19–26 μ × 35–90 μ (Fig. 2).

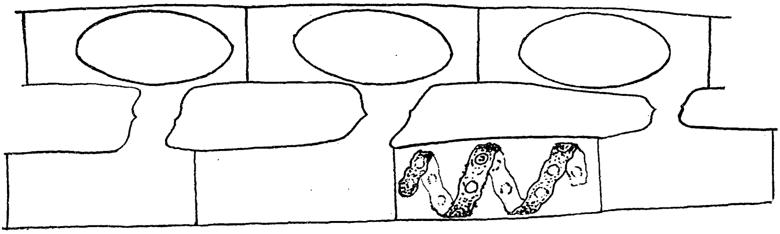

FIG. 2 Typical *S. communis* showing form of zygospore, sporiferous cell and sterile cell.

The collections in question showed in addition to the typical filaments others with the characters of *varians*,

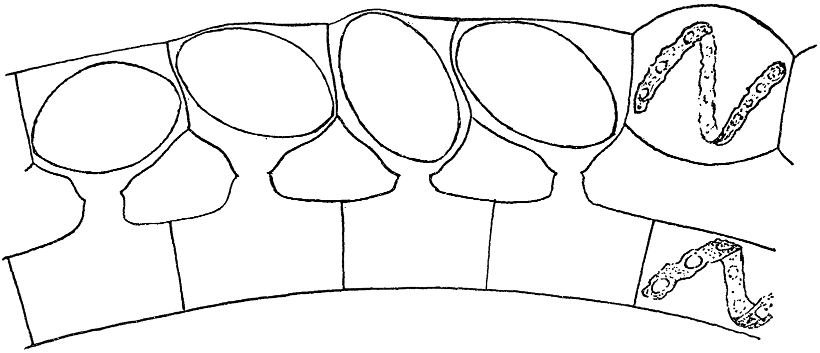

Fig. 3. *S. varians* × *S. communis* showing dimensions of communis, otherwise resembling *varians*.

but with dimensions similar or near to *communis* (Fig. 3) and still others with the form characters of *communis*, but the dimensions of *varians* (Fig. 4). The figures are camera drawings all made from Coll. No. 1877, May 27, 1913.

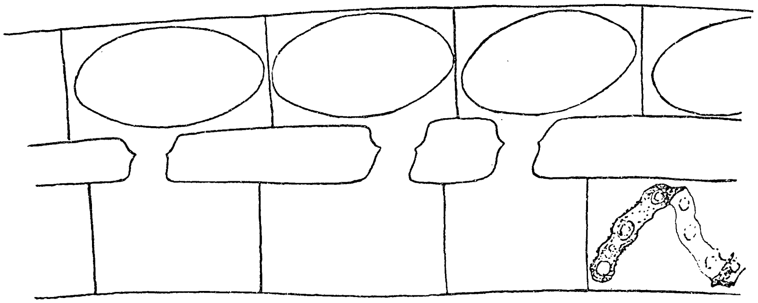

Fig. 4. *S. varians* × *S. communis* showing dimensions of varians, otherwise resembling *communis*.

Spirogyra varians × *S. porticalis*

In collections from a small stream that flows under the Clover Leaf R. R., just east of the station at Lerna, Ill., collections made during May, 1913, and April, 1914, *Spirogyra varians* was found conjugating with *S. porticalis*. Accompanying the typical *varians* and *porticalis* filaments were fruiting filaments which could not be placed satisfactorily in either species, but which possessed various combinations of the characteristics of both species.

In collections from Cossel Creek, about one mile west of Charleston, Ill., made during May, 1914, and April, 1915, a similar mixture of forms was found associated with filaments of typical *varians* and *porticalis*. It was the discovery of these latter collections in 1915 that led me to go over the collections from Campus Creek, Lerna, and the previous collections from Cossel Creek. In all cases the forms seemed quite explicable on the assumption that hybridization had occurred in previous years as it was occurring when the collections were made and that the progeny of the hybrid zygospores showed various combinations of the characteristics of the parent species.

FERTILIZATION IN SPIROGYRA

Fertilization in *Spirogyra* takes place by the fusion of two gametes through a tube formed by the union of emergences from two adjoining cells in the same or different filaments. The zygospore matures its wall within three or four days after the passage of the gametes.

In the large species, *S. ellipsospora*, I have watched the movement and fusion of the gametes. The male gamete withdraws slightly from the gametangium wall; its chromatophores disintegrate and the whole gamete appears to have a foam structure. Opposite the tube a small lobe develops and this moves through the tube to the female gamete. On reaching the surface of the female gamete the cytoplasm of the female gamete at the point of contact spreads, drawing its chromatophores apart. The male gamete penetrates the cytoplasm and at the end of the process lies entirely inside the female gamete. Its chlorophyll then turns brown and stains the cytoplasm, so that it can be seen through the maturing spore wall for several days. During this period it gradually spreads out and coalesces with the cytoplasm of the female gamete.

Since the cytoplasm that secretes the zygospore wall is thus only the cytoplasm of the female gamete, its form and markings are determined entirely by that gamete.

All the recorded facts concerning hybrid zygospores are in harmony with this observation.

The male and female nuclei, however, do not fuse until some time later, perhaps two to four weeks. The character of the zygospore is therefore entirely dependent upon the female parent. This is well brought out by all the published figures of hybrid zygospores as well as by my own observations. After the formation of the fusion nucleus various observers—Chmielewski (1890), Tröndle (1907), Karsten (1909) and Kurssanow (1911) (*Zygnema*)—report the occurrence of a double mitosis of which the second division is heterotypic. This results in the formation of four nuclei, of which three degenerate (Tröndle, 1911). The degeneration of three of the nuclei has been observed also by Kurssanov in *Zygnema*. The remaining nucleus becomes the final nucleus of the zygospore.

In a hybrid zygospore, therefore, the first fusion nucleus would contain the hereditary factors for the alternate characters of both species; in the subsequent reduction division and degeneration of three of the nuclei the final zygospore nucleus would contain one of the several possible combinations of these hereditary qualities. The vegetative filament derived from a hybrid zygospore would present some combination of its vegetative characters, such as cell dimensions, number of chromatophores and character of the end walls. The factors for spore characters would not become visible until it conjugated, and then only the characters carried by the female filaments would become visible since the spore characters are entirely matriclinal. In the adjoining diagram (Fig. 5) the zygospores are figured in typical forms. The two characters most important in separating the species are: (1) The dimensions of the filaments (*varians* averages about 33, *communis* about 22); (2) the lateral inflation of the sporiferous cell in *varians* in contrast with the cylindrical sporiferous cell of *communis*. If we represent the factor for the dimensions of *varians* by *A* and of *com-*

munis by *a,* and the factor for the inflated sporiferous cell of *varians* by *B* and cylindrical sporiferous cell of *communis* by *b,* then the fusion nucleus in the zygospore would have the composition *AaBb.* At the subsequent reduction division these four characters might be distributed in four different ways: *AB* typical *varians; Ab varians* dimensions and *communis* type of sporiferous cell; *aB*—*communis* dimensions and *varians* type of sporiferous cell; and *ab*—typical *communis.* All four of these possibilities are represented by filaments in Collection 1877 from Campus Creek. Furthermore, the fertile cells of individual filaments and the zygospores formed are similar throughout a particular filament, as would be expected on the basis of the origin of the final zygospore nucleus. This hypothesis, therefore, accounts for all the facts at present known concerning this series of collections.

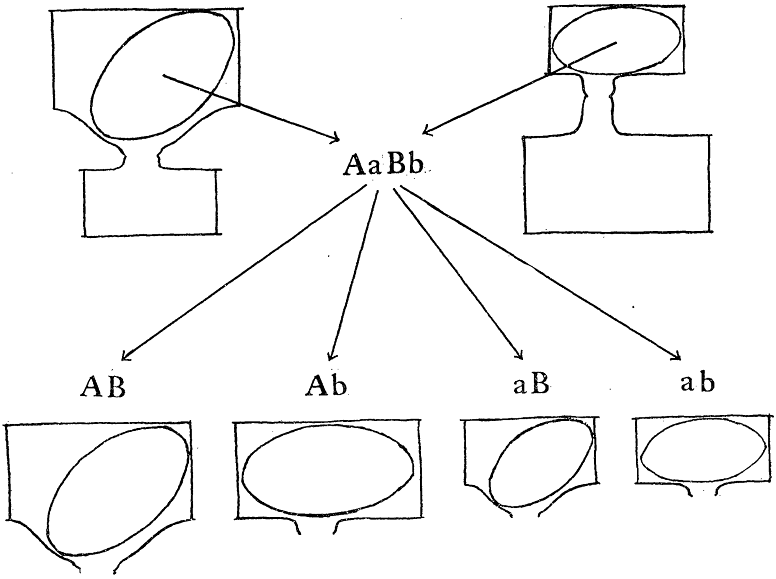

FIG. 5. Diagram illustrating the hybrid progeny of a cross between *S. varians* and *S. communis.*

The forms occurring in the two series of collections from Lerna and Cossel Creek can be similarly accounted for. In this case, however, the two species, *S. varians* and *S. porticalis,* evidently differ in three characters. The characteristics of *varians* have been given above.

S. porticalis (Fig. 6) has vegetative cells 40–50 $\mu \times$ 66–200 μ containing a single chromatophore, making three to four turns. The fertile cells are cylindrical and the zygospore is ovoid, 38–50 $\mu \times$ 50–83 μ. It, therefore, differs from *S. varians* in dimensions of the vegetative cells, in the absence of inflated fertile cells, and in the ovoid form of the zygospore. In both series of collections all of the eight possible combinations of these three characters occur.

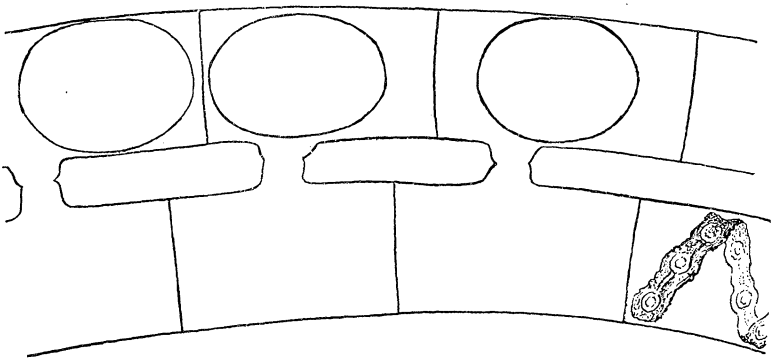

FIG. 6. Typical *S. porticalis* showing single chromatophore, ovoid spores and cylindrical sporiferous cells.

In the accompanying diagram (Fig. 7) the dimension factor for *varians* and *porticalis* are represented by *A* and *a,* respectively. The factor for the *varians* type of fertile cell by *B,* and for the *porticalis* type by *b.* The factor for the ellipsoid spore by *C* and for the ovoid spore by *c.* The nucleus formed by the fusion of the two gamete nuclei therefore contains all the factors (*Aa, Bb, Cc*). The final zygospore nucleus contains any one of eight possible combinations: *ABC,* typical *varians; AbC, varians* dimensions and spore form, with *porticalis* fertile-cell form; *Abc, varians* dimensions, with *porticalis* fertile-cell form and spore form; *ABc, varians* dimensions and

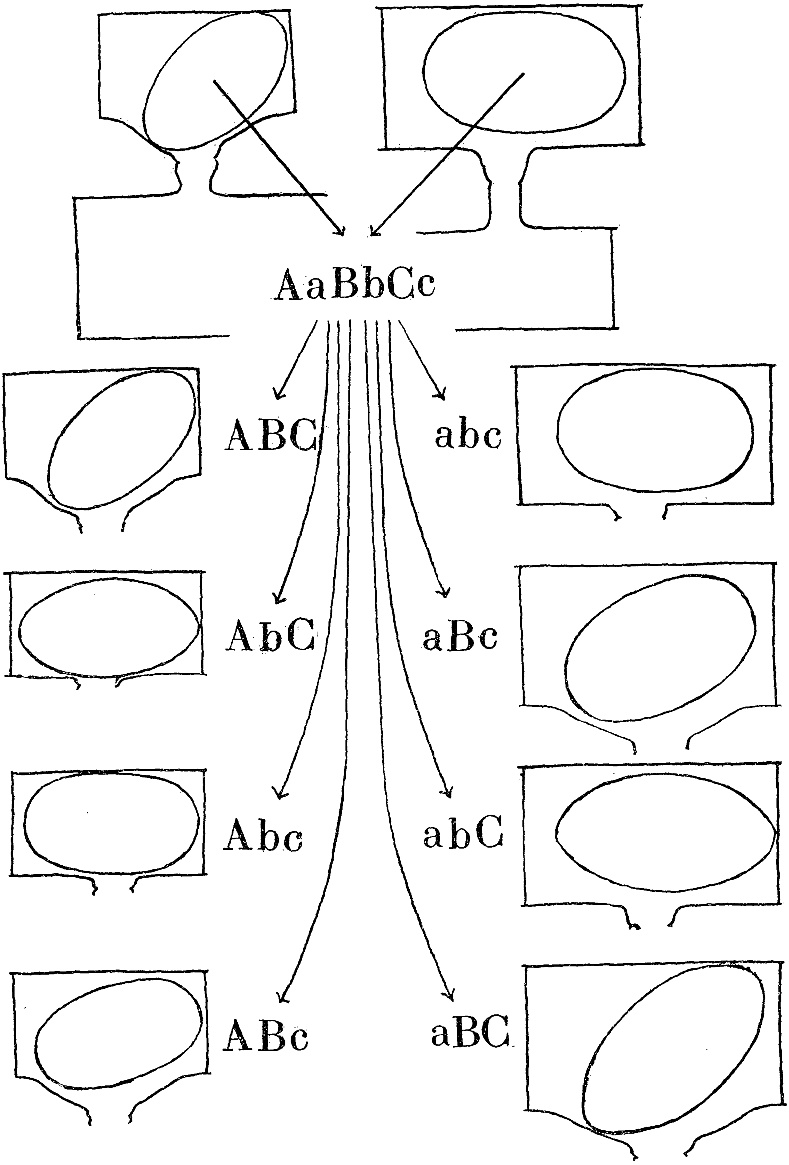

FIG. 7. Diagram to illustrate hybrid progeny of a cross between *S. varians* and *S. porticalis*.

fertile-cell form, with *porticalis* spore form; *abc,* typical *porticalis; aBc, porticalis* dimensions and spore form, with *varians* fertile-cell form; *abC, porticalis* dimensions and fertile-cell form, with *varians* spore form; *aBC, porticalis* dimensions, with *varians* fertile-cell and spore form.

The female filaments derived from these several zygospores should show these eight possible combinations when they fruit. These forms have all been found in the two series of collections in each of two successive years, and there seems to be no question but what they are the products of hybridization and segregation. Since the inheritance is entirely matriclinal, segregation occurs in the first generation.

As to the relative numbers of the several types it is impossible to count filaments in a collection. Theoretically they should be present in about equal numbers if all the filaments are of hybrid origin. In all the collections, however, there were filaments conjugating in the usual way, so that any attempt at counting filaments would be useless even though it were practically possible.

SUMMARY

1. Hybridization between *Spirogyra communis* and *S. varians* and between *S. varians* and *S. porticalis* have been observed. The forms probably derived from these crosses have also been found.

2. Hybrids are exceedingly rare among species of *Spirogyra.*

3. They have been observed only in a few species.

4. Hybrid zygospores may be formed between species even though they have very different vegetative and spore characters.

5. The nuclei derived from the two gametes do not fuse until after the zygospore wall matures. The form of the zygospore is determined entirely by the female gamete.

6. The fusion nucleus of a hybrid zygospore contains factors for all the various characters of both species.

When the reduction division takes place these factors are segregated in various combinations in the final spore nucleus.

7. When the filaments derived from hybrid zygospores fruit their hybrid character becomes evident in the dimensions of the filament, the character of the sporiferous cell and the form of the zygospores.

8. Inheritance is matriclinal and therefore the segregation becomes evident in the first generation.

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